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Relation of Temperature and Moisture to Brood Development of the Western Pine Beetle

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Abstract

A laboratory study on brood development of the western pine beetle was conducted during the past winter in the Bureau of Entomology Laboratory at Berkeley, California. It is supplementary to similar brood studies made in the field on this insect during the past two years.

Western yellow pine blocks were brought in from the field and caged with infested bark for attack. The blocks were then distributed in constant temperature compartments ranging from 35 to 106 degrees F. In these chambers brood development was observed and records on temperature and phloem moisture were obtained. Over 5000 larvae were obtained for the study by shaving up infested bark. They were sorted and grouped in lots of known numbers (50, 75 and 100) and subjected to constant temperatures for further observations on development. Tests were also made on a large number of larvae alternating the groups for a different number of hours daily between a low limiting temperature and a high optimum temperature. Subsequent development was observed and recorded. Eggs were isolated and incubated at a range of low temperatures to determine the lowest point at which they could hatch.

The western pine beetle developed very poor broods under the entire range of temperature and moisture conditions obtained on blocks in the laboratory and slash in the field. Brood development of this insect began very close to 50 degrees F. and increased directly with the temperature up to about 85 degrees. The temperature at which the greatest percentage of insects were able to complete normal development was about 75 degrees F. while the temperature at which development took place with the greatest velocity was 10 to 15 degrees above this. Temperatures below 50 degrees resulted in no development over a period of nearly 50 days. We have therefore referred to 50 degrees F. as the threshold of development. Constant temperatures of 95 degrees and above usually proved fatal to all stages of this insect.

Constant temperatures of 85 degrees F. gave the maximum rate of brood development with a single exception where brood matured more rapidly at 95 degrees. Brood development at a constant temperature of 75 degrees progressed more slowly than at 85 degrees but survival was usually better at the lower temperature. At constant temperatures of 65 degrees the rate of development decreased materially. Some development was apparent at constant temperatures of 55 and 52 degrees F. but constant temperatures of 48, 40 and 36 degrees permitted no apparent brood development altho the brood remained alive in all stages and the adults were feebly active becoming normally active when warmed to room temperatures.

The phloem moisture of the infested blocks either remained nearly constant or increased throughout brood development in all cases except at temperatures of 100 degrees or higher. It was abnormally high at all times averaging from 200 to 300 per cent in all but the blocks at higher temperatures.

Tests with about 3000 mature larvae indicated that the rate of development of the more nearly mature brood depended directly upon the hour-degrees of effective temperature above the threshold of development. In other words, a definite number of cumulative day or hour-degrees of temperature was necessary for the completion of a specific stage in the life history. As determined by the development from pupae to adults it was found to be slightly over four thousand hour-degrees.

Brood mortality in blocks under controlled temperature conditions was heaviest in the young larval stages. A green fungus* was almost invariably associated with the decaying bodies of the dead larvae. What appeared to be dwarfed or stunted larvae tunneled about in the inner bark of some blocks over periods of six and seven weeks and formed abnormally long winding larval galleries. Eggs hatched at approximately the same temperatures at which larval and pupal development began.

Introduction

Studies on brood development of the western pine beetle (Dendroctonus brevicomis Lec.) have been conducted during the past two summers within a range of temperature and moisture conditions limited to those which could be obtained in the field. During the past winter these studies were continued in the laboratory at Berkeley, California, where more accurate control of the conditions affecting insect development was possible.

Largely through the suggestions and assistance of Mr. J. M. Miller and other members of the Berkeley Station a creditable showing was made on the study during the time spent on it. Mr. R. N. Jeffrey continued the studies on a second series of infested blocks during April and part of May after the writer had returned to the Portland office.

Temperature and its effect upon the development of plant and animal life has probably been more thoroughly studied than any other single factor. Miller* has contributed an outstanding paper on fatal high and low temperatures for the western pine beetle. Little information has been published relative to the temperatures necessary for brood development of this insect. However the importance of temperature as applied to field conditions has been fully appreciated as evidenced by the following general note taken from the brood records at Ashland, Oregon. "Overwintered broods in the south side of a tree may emerge from 27-41 days earlier than on the north side of the same tree and average 35 days earlier. Broods in trees of the first seasonal generation which emerge during the summer months and do not overwinter, appear to develop at about the same rate on all sides of the tree". In this phase of the study we were able to determine a few points here-to-fore unknown regarding the effect of temperature upon development and activity of brood stages of the western pine beetle.

*Miller, J.M., High and low lethal temperatures for broods of the western pine beetle.

Moisture, or in the case of most insects atmospheric humidity, has in the past received much less attention than temperature. Because of the little possible effect of atmospheric humidity on broods of the western pine beetle the term moisture will be used in this report as referring to moisture of the phloem. Since this media and food supply is usually in a more or less saturated condition and completely surrounds the insects the moisture content of this layer of inner bark should reflect the moisture conditions to which the insects are subjected. Unfortunately control of phloem moisture even in blocks of wood in the laboratory has not been possible, and we have therefore been forced to record the moisture as we have found it.

The object of the study was to determine the effect of temperature and moisture in limiting the development of western pine beetle broods and the optimum conditions for brood development. Such knowledge is important in helping us to recognize the general climatic conditions which favor or retard western pine beetle epidemics from one year to another and the conditions in slash which are favorable or unfavorable for brood development.

This report supplements the studies on brood development previously reported by the writer in station reports of 1930 and 1931, and it is hoped that the information presented herein may add something further to our knowledge of the activities of the western pine beetle.

Materials and Methods

The equipment used in the laboratory study was essentially the same as that used in the field except for the addition of constant temperature controlled compartments.

Temperature equipment.

Through the courtesy of the University of California and the efforts of Mr. Miller, constant temperature cabinets were either borrowed or built for the purpose of housing infested pine blocks during the brood development study. In this way a series of temperatures ranging from 35 to 106 degrees Fahrenheit were obtained. The low temperature frigidaire machine was also used in part of the work. Space in chambers kept at constant temperatures of 36, 40, 48, and 52 degrees F. were loaned to us by the University. Two other cabinets with high temperatures of 86 and 104 degrees were also loaned for the first tests but were not used during the second. Space with temperatures around 60, 65 and 70 degrees was obtained by manipulation of storage and office space in Giannini Hall. Temperature constants of 75, 85, 95 and 100 degrees were made possible through the construction, by Mr. Wagner, of a four chambered cabinet wired for electric heating bulbs and ventilated by the use of two small sliding doors in the main door of each chamber. This cabinet was kept in the cork lined constant temperature room so that better regulation of it would be insured. A small electric fan was used in the large chamber to increase ventilation and to insure the same amount at all times. After the compartments of the cabinet were once regulated, they operated within a range of plus or minus 2 degrees and usually less.

Standard Fahrenheit thermometers were used to check the temperatures of all compartments used and to follow temperature lag in the jars when transferred from one temperature to another. All temperature determinations were made on the Fahrenheit basis. The thermometers were graduated from -10 to 220 degrees.

Thermographs were set up in all but the smaller thermoregulated compartments so that complete temperature records were obtained. Three of these machines were borrowed from the California Forest Experiment Station. In rooms already equipped with machines the records were copied.

<u>Moisture equipment</u>

Phloem moisture was determined on the dry weight basis. Phloem samples were collected weekly in tight jars, weighed as soon as possible and dried in a drying oven for three hours. Because of the necessity of taking small samples uniform weights 4-6 gms were used in all cases and both weighings were made on finely adjusted laboratory balances. Mr. R. S. Jeffrey assisted materially in running the moisture determinations.

<u>Cage equipment</u>

A large cage was constructed in sections and brought into the laboratory for the purpose of caging infested bark and pine blocks. The cage (about 4½ x4½ x4½ feet) (Fig.2) was built by Wagner and constructed so that one side could be easily removed and blocks placed within or removed. It was placed on roofing paper and the bottom and edges lined with cotton batting to prevent the beetles from escaping. The reason for bringing this cage into the building was to take advantage of the room temperature and to accelerate beetle development, emergence and attack.

<u>Logs and insects</u>

A large quantity of infested bark containing mature larvae and two dozen short log sections (2 ft.) (Fig. 1) were collected in the field at Klamath Falls and shipped to Berkeley for the beginning of the work. When this supply had been exhausted more (logs 2 ft.) material was collected during a short trip to the Stanislaus National Forest. Other shipments of infested bark were received from Jack Wagner, Ranger, of the Sequoia National Park and from W. Hale of Weyerhaeuser Timber Company. The infested bark was used as needed. Some was kept at low temperatures for future use and some placed at high temperatures for early emergence. Extra pieces were stored in the open on the north side of a building until needed.

<u>Miscellaneous</u>

Petri dishes, jars and improvised boxes were used to contain brood of different stages for some of the experiments. (Fig.3).

Procedure

Bark infested with brood of the western pine beetle was collected in the field and caged in the laboratory for beetle emergence. Western yellow pine logs averaging two to three feet in length and ten to eighteen inches in diameter were shipped in from the field and caged with the emerging beetles. As soon as examinations showed that attack had been established on a pair of blocks they were immediately transferred to one of the constant temperature compartments and weekly moisture and brood records were made on one of the blocks, the other being kept for the final examination. Two complete sets of two blocks each were run in all available chambers.

Over five thousand mature larvae were obtained by shaving up infested bark and were used to determine the influence of temperature on rate of development of later brood stages. A daily schedule for transfer of these larvae was worked out so that different groups received different duration of exposure to optimum temperatures each day. Subsequent brood development was observed and recorded daily. Other groups of mature larvae were placed in the different constant temperature compartments and the rate of development noted weekly.

Eggs were dug from recently attacked blocks and isolated on moist blotting paper in petri dishes and these lots distributed in the compartments of lower temperature range in order to determine the lowest temperature at which they could hatch. (Fig. 8).

Western Pine Beetle Brood Development

The laboratory work on brood development of the western pine beetle was divided into two phases. First the development of brood within the infested blocks, and second the development of the more advanced brood obtained from infested bark. Part one of the study more nearly simulated conditions as found in felled logs and slash. It began with the attack and continued through the egg, larval, pupal and adult stages or as long as the brood remained alive. Part two had the advantage of permitting accurate isolation of a known number of larvae and of better observation of development through daily examination. This part of the study continued until the insects either reached the adult stage or were lost through mortality. This phase supplements the first one but in many respects gives us more definite information than could be obtained through examination of broods within the blocks.

Each temperature used will be discussed separately and not grouped as they were in graph II which indicates weekly phloem moisture of the infested blocks. In this case the two sets of experiments were averaged because the slight differences in phloem moisture of two series of blocks at similar temperatures did not warrant individual presentation.

Brood development in infested blocks

A presentation of western pine beetle brood development in infested blocks kept at constant temperatures will be found in table 1.

Table I. Western Pine Beetle Brood Development in Infested Blocks Kept at Constant Temperatures.

Temperature degrees Fahrenheit	1st week Moist. %	1st week Brood	2nd week Moist. %	2nd week Brood	3rd week Moist. %	3rd week Brood	4th week Moist. %	4th week Brood	5th week Moist. %	5th week Brood	6th week Moist. %	6th week Brood	7th week Moist. %	7th week Brood
102-106	—	Active parent adults	187	All dead	167									
98-102	153	Eggs hatched	139	Larval mortality heavy	167	All dead	98							
93-97	—	Eggs hatched	278	Some larval mortality few 1/4-1/2	259	Larval mortality heavy some 3/4	241	Larva 1/2 1 callow adult	232	No brood		Few small larvae		
93-97	189	Eggs hatched	180	Some larval mortality few 1/2	187	Larval mortality heavy	167	Larval mortality heavy dead p. adults	191	Larval mortality heavy				
84-88	—	Eggs hatched	256	Some larval mortality	277	Heavy larval mortality. Some	308	No brood found	294	Larval mortality heavy.				
83-87	206	Eggs hatched	215	Light mortality some 1/8	204	Heavy lar. mor. larvae 1/4	177	Few [illegible] larvae	209	[illegible]				
75-77	194	Eggs hatched	216	Small larvae	214	Larval mortality some 1/8	202	Larval mortality heavy larva 1/2	234	All dead				
65-75	222	Eggs hatched	225	Tiny larvae	290	Heavy mortality	[illegible]	Few living larvae	266	50% mortality larvae 1/2				
65-75	—	Eggs hatched	266	Small larvae	276	Brood light larvae 1/4	262	Few small larvae one small pupae	269	1 new adult 1 small pupae few small larvae				
56-65	286	Eggs	279	Eggs hatched	296	Small larvae	—	Some mortality larvae 1/8	—	Some mortality larvae 1/4	—	Few larvae 1/4	182	Few small larvae
56-65	250	Eggs	226	Eggs hatched	243	Larvae abundant	242	Mortality light larvae 1/8-1/4	255	Mostly living larvae 1/4	259	Few larvae in inner bark	224	Heavy larval mortality 1/2 small larvae
50-54	189	Eggs	214	Eggs	224	Eggs hatched	209	Larvae small	241	Larvae small	241	Larvae small some devel.	224	Larvae small

Table 1. Cont'd. Western Pine Beetle Brood Development in Infested Blocks Kept at Constant Temperatures.

Temperature degrees Fahrenheit	1st week		2nd week		3rd week		4th week		5th week		6th week		7th week	
	Moist. %	Brood	Moist. %	Brood	Moist. %	Brood	Moist. %	Brood	Moist. %	Brood	Moist. %	Brood	Moist. %	Brood
45-50	—	Eggs	249	Eggs	276	Eggs	278	Eggs	260	Eggs	297	Eggs		Eggs
36-38	—	Eggs	252	Eggs	249	Eggs	246	Eggs	220	Eggs	212	Eggs		Eggs

Broods subjected to constant temperatures of 102 to 108 degrees F. were of short duration. Heavily infested blocks subjected to this temperature contained, at the end of five days, only dead parent adults (fig. 7) and unhatched eggs. The adults pushed out sawdust for a short time after being in this chamber, but no activity or development could be found after the first week. The slight reduction in phloem moisture (20 per cent) in these blocks during the first week could not conceivably have any bearing on the brood mortality. It is therefore attributed to high lethal temperatures.

Brood in infested blocks subjected to constant temperatures of 98 to 101 degrees lasted but two weeks longer than at the higher temperature. Some of the eggs hatched during the first week, and the adults were active. However, heavy mortality occurred among the young larvae during the second week, altho some larvae were recorded as one fourth mature. During the following week the mortality extended to include all larvae as well as the parent adults (fig. 7). A green fungus was associated with some of the dead larvae. Phloem moisture decreased but slightly (10 per cent). The fact that both the adult and larval mortality occurred at about the same time indicates that here too mortality should be attributed to high temperature.

Two series of blocks were run at temperatures of 93 to 97 degrees, but because of differences in these tests they will be discussed separately. The first test at this temperature produced one callow adult in 27 days, the shortest time recorded for brood development of this insect. However, brood mortality in these blocks was heavy, and most of the brood found appeared as under-sized, under-nourished, rat-tailed larvae. The final examination at the end of six weeks showed a few small larvae burrowing around in the inner bark but no emergence. Phloem moisture varied but little, remaining high throughout the experiment. Here with an example of complete development (egg to adult) in 27 days at constant high temperature and continued high phloem moisture content the reason for failure of most of the brood has been obscured.

In the second series of blocks at 93 to 97 degrees brood development appeared to progress rapidly during the first week. Then as with higher temperatures mortality was extremely high during the second and third week (fig. 8). Parent adults were found dead at the end of four weeks. A very few small larvae were still burrowing in the inner bark after the fifth week, but no other brood could be found. Here, too, the green fungus was associated with the dead larvae. It was found on them in both inner and outer bark. Phloem moisture remained high but almost constant during the period covered by the examinations. If based alone on the results of the observations the cause of brood failures in the blocks cannot be determined. However, this temperature was found to be too high for proper development of brood in the advanced stages and is therefore probably the most important limiting factor in this case.

At constant temperatures from 84 to 88 degrees the parent adults were very active, the hatching of most of the eggs and abundance of active small larvae looked like the beginning of a good brood. By the end of the second week larval mortality began and was so heavy that after three weeks no brood was found until the final examination revealed a few small

larvae working in the cambium. A second test with the chamber operating between 83 and 87 degrees gave results so similar to the one just described that no discussion of it is necessary. Here, too, brood which appeared heavy and thrifty at first, gradually disappeared until at the end of four weeks almost no brood could be found, and that which did exist occurred only as small larvae. Phloem moisture decreased very little in the two series of blocks during the experiment. It remained high at all times, staying between 200 and 250 per cent.

Constant temperatures of 73 to 77 degrees resulted in a somewhat slower rate of brood development than higher temperatures, and the larvae lived on an average of about a week longer. Heavy brood occurred as larvae during the first three weeks. Slight mortality appeared the third week, and by the end of the fourth only an occasional living larva could be found. Phloem moisture remained between 200 and 234 per cent during this period. Here again it is evident that this temperature which has been shown to be very favorable for broods of the western pine beetle could have had no part in the resulting mortality.

Two tests at room temperatures which fluctuated between 68 and 75 degrees and averaged about 70 degrees gave slightly varying results. In the first test some brood reached maturity. At the end of the fourth week one small pupa was found, and two weeks later at the final examination, one new adult, one small pupa, and a few small larvae were present. Of outstanding significance is the minute size of the pupae and adults found in these blocks. They were much smaller than the smallest specimens obtained from the infested bark. Phloem moisture remained slightly above 250 per cent throughout the experiment. The second series of infested blocks run at the above temperature did not produce either pupae or adults, but one half grown larvae appeared in five weeks. As before, larval mortality was high during the fourth week. Phloem moisture varied only slightly less than in the preceding blocks.

In a room with temperature fluctuating between 55 and 65 degrees and averaging 60 degrees, almost all of the young larvae remained alive for four or five weeks. Only slight mortality occurred up to this time, but development was also much slower than in preceding cases. At this time larvae from one eighth to one fourth grown were abundant. During the following three weeks brood mortality increased so that at the final examination at the end of seven weeks only a few tiny larvae remained (fig. 4). Phloem moisture in these blocks increased from about 225 to nearly 300 per cent.

One series of infested blocks subjected to very accurately controlled temperatures fluctuating occasionally and only for very short periods from 50 to 54 degrees, but for the most part remaining practically at 52 degrees showed very slow brood development. Eggs hatched at this temperature at the end of three weeks and small larvae remained as such with only slight development during the next four weeks. This is the lowest temperature at which apparent brood development occurred. Phloem moisture increased from about 200 to 240 during the study.

Blocks containing parent adults and eggs of the western pine beetle, placed in a low temperature chamber where temperatures varied from 45 to 55 degrees, showed no brood development in seven weeks. During the first three weeks the temperature remained below 50 degrees. Later it increased for short periods to as high as 55 degrees, but the average and most common temperature recorded in the chamber during these observations was about 4[illegible] degrees. Adult beetles were able to walk slowly at this temperature. In these blocks phloem moisture increased from about 2[illegible] to nearly [illegible] per cent. Here it is believed that low temperature prohibited development.

A still lower series of infested blocks was run at a constant temperature of 34 to 38 degrees, but after seven weeks the eggs still remained unhatched. At 3[illegible] degrees parent adults were barely capable of slow movement of legs, but they could not walk. When removed to room temperatures they recovered very quickly and appeared unharmed by long exposures at these temperatures. Eggs from this material when transferred to room temperatures hatched within a few days. Here phloem moisture decreased from 25[illegible] to 210 per cent. The only other decreases obtained were in blocks at high temperatures. With the last series the absence of development is the result of low temperatures.

<u>Development of advanced brood obtained from infested bark</u>

In order to supplement brood development studies in infested blocks some fifteen hundred mature larvae were dug from infested bark brought in from the field during the winter months. These larvae were mixed in order to distribute any influence of previous development, and all except prepupal larvae were discarded. A given number were then selected for brood development tests, imbedded in finely ground outer bark from which they had been taken and then distributed in jars in the various constant temperature compartments and subsequent rate of development carefully followed. These tests were duplicated for the purpose of insuring more accurate data than could be had from a single test. The results of these experiments are shown in graph III. Here temperatures have been grouped for graphic presentation but will be specifically discussed.

Constant temperatures from 10[illegible] to 106 degrees resulted in complete larval mortality within five days. Those from 9[illegible] to 102 gave similar results within ten days. These results agree with those obtained from the infested blocks at the same temperature.

At constant temperatures 93 to 97 degrees a few larvae transformed to pupae at the end of four days, although larval mortality was apparent within the jars. Within 10 days all larvae and all pupae succumbed to this temperature.

Jars of mature larvae in constant temperature chambers ranging from 83 to 87 degrees showed the first good brood development. At the end of two days pupae began forming and adults appeared after six days

exposure. Within twelve days the jars contained only young adults and dead larvae and pupae. Mortality was high, being 52.2 per cent, but development of the brood which survived was rapid.

Constant temperatures 73 to 77 degrees resulted in slower development of the brood than at the preceding exposure. Pupae appeared as early as before (two days), but final adults appeared five days later than those at the higher temperature (17 days). At the lower temperature mortality was slightly less, being 44.1 per cent.

Development continued to slow up at lower temperatures. In a room varying from 65 to 75 and averaging 70 degrees, first pupae were observed at the end of two days, but the pupal period was prolonged to 23 days when the last adult appeared. A mortality of 30 per cent in this case was the lowest obtained in any of the tests with advanced broods.

A marked decrease in rate of brood development occurred within a constant temperature chamber running at 58 to 63 degrees with an average of 60 degrees. First pupae appeared in six days as against two in previous cases, and first adults in 26 days. It required 42 days for final adults to transform to pupae, and during this time mortality reached 54 per cent.

A jar of larvae placed at 50 to 54 degrees remained there for 14 days before one of them pupated. At the end of 42 days when the experiment was discontinued, approximately one third of the living insects had pupated. Mortality in this jar was 46 per cent.

Larvae in jars placed at constant low temperatures of 38 to 42 degrees and 34 to 38 degrees for 47 days were, to all outward appearances, about the same as when entered. No apparent development had occurred. A 40 per cent mortality resulted over this period.

Tests with recently laid eggs of the western pine beetle showed that temperatures necessary for incubation, hatching and early larval development corresponded very closely to those necessary for development of other stages. Two hundred fifty eggs were isolated on moist blotting paper in covered petri dishes (50 per dish) and distributed at constant temperatures of 36, 40, 52, 55, and 60 degrees respectively in order to determine the lowest temperature at which they would hatch. Within a period of 16 days 20 young larvae occurred at 60 degrees, 14 at 55 and 7 at 52 (fig. 5). Altho the remaining dishes at 40 and 36 were left for further study no eggs hatched within them during a period of three weeks. This corresponds closely with records on eggs within the infested blocks and also with development of other brood stages.

Two hundred mature larvae were divided into lots of 50 each and placed on blotting paper in petri dishes to check the effect of humidity on survival and development. Dry blotting paper was used in two dishes and wet in the other two. A wet and a dry group were placed at a constant temperature of 95 degrees and a similar set put into the chamber kept at 100 degrees. It was thought that the moisture might prolong the survival of the insects in the wetter dishes. These two series were examined

daily for five days, but no difference in mortality could be noted. At the end of this period mortality was almost complete in all dishes. Mold in the dishes with wet blotting paper developed extensively on the larvae while those under drier conditions appeared to have suffered mortality through heat and dessication. The wet larvae turned very black and swelled. The dry larvae shriveled and turned to a yellowish color.

Discussion

Either with young brood in infested blocks or more advanced brood from infested bark, it is apparent that temperature plays a very important part in determining the rate of brood development. With both sets there was no apparent brood development at temperatures below 50 degrees. Above 50 degrees the rate of brood development increased with the temperatures until the point was reached where lethal temperatures caused death. The most rapid brood development occurred just before lethal temperatures were reached.

Moisture was practically constant in the test blocks and was always high, averaging from 200 to 300 per cent. Similar conditions are found in slash in the field and apparently is not conducive to good brood development.

The mortality which occurred in the laboratory tests cannot be fully explained. With mature larvae in dry powdered bark 30 per cent or more mortality occurred. This might have been due to handling, to change in environmental conditions or to dessication. Since most mortality occurred during stages of transformation from larvae to pupae and pupae to adults it is believed that dessication prevented these delicate changes. Larvae with split head capsules and skins which failed to slough off were common. Also pupae whose wings appeared to stick fast in place, thus preventing complete transformation to adults, were common. Mortality in advanced broods under favorable temperatures except at these critical points was seldom found. For temperatures of 95 degrees or over complete mortality was evidently due to lethal temperatures. This idea was further supported when similar rates of mortality occurred at these temperatures in groups of mature larvae kept under either wet or dry conditions.

With the immature larvae in the logs the higher mortality must be due to either one or all of the following causes:

Excessive phloem moisture of 200 to 300 per cent which invariably obtains in logs and slash kept within the temperature limits for brood development may be responsible either directly or indirectly for a large share of the brood mortality. We know that in standing trees where brood development of the western pine beetle proceeds normally there is rapid loss of moisture which accompanies good brood development. On the other hand, in logs and slash where broods of this insect fail to develop properly there is an increase in phloem moisture. Similarly brood in infested blocks was subjected to the higher moisture conditions, while that in the jars where more successful development occurred were exposed only

to the dry media of pulverized outer bark. Whether the effect of excessive moisture was direct or indirect is unknown, however, phloem moisture content and brood failures appear to be so closely related that one may be used as an indicator of the other.

The theory that nutritional disturbance may be largely responsible for brood failure of this insect is rapidly winning support. Preliminary experiments by Jeffrey* working on felled logs both in the field and under laboratory conditions indicate that very important food changes occur in the inner bark soon after cutting. He finds that certain sugars appear to increase slightly at first and then to decrease within a few days to practically nothing. In the experiments on brood development there is much evidence supporting the theory of the importance of malnutrition in brood failures. Comparing the two sets of experiments previously discussed the larvae in the logs were in the active feeding stage and were dependent on the inner bark for their nourishment. The mature larvae in jars had completed their feeding in standing trees and were no longer dependent upon food for their existence or further development. Changes in nutritional value of the food would therefore be reflected in the success or failure of brood in the blocks but not in that of the advanced larvae. The half-starved, under-nourished, rat-tailed appearance of the larvae in blocks; the fact that they make abnormally long winding larval galleries, as if in search for food; the unusually long period spent in the inner bark, and the slow death of many of them all support the theory of insufficient nourishment.

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*Jeffrey, R. W., The concentration of certain sugars in the bark of the western yellow pine as relates to western pine beetle attraction. Sta. Rep. 1930 Ber. Cal.

The activity of fungi associated with the dead broods invariably commanded attention. A green fungus identified by Wagener* as a <u>Penicillium</u> was particularly abundant in the larval galleries where the brood had failed. Whether this fungus plays a part in the death of the larvae or whether it merely finds good growing conditions on the bodies of dead larvae is not known. However, because of the generally saprophitic nature of this group of fungi it is believed to be of little importance in the death of the insects.

Effect of cumulative temperatures

A second phase of brood development studies using brood in the more advanced stages was conducted, using some three thousand mature larvae. These experiments were designed to determine the number of daily effective hours necessary for beginning of development of hibernating broods. Other points to be determined were rate of development as influenced by cumulative temperatures and whether or not alternating temperatures stimulated brood development.

*Wagener, W. W., Office of Bureau of Plant Industry, San Francisco, Calif.

Hibernating larvae from infested bark were obtained and sorted as previously described and placed in numbered containers (fig. 4) which were altered from constant temperature 40 to 75 degrees for a given number of hours daily. Since 40 had been found to be below the threshold of development, a compartment at this temperature was used in which to keep all broods when not at 75 degrees, which was the temperature selected for good development. Brood development was assumed to have occurred only during the hours spent at the higher temperature. The tests were run three times, using on each occasion eleven jars containing 50 mature larvae. One test of eleven jars containing half grown larvae was tried, but because of excessive brood mortality was discontinued. In this lot of larvae feeding had apparently not been completed. A fourth series was run using infested bark containing half grown larvae, many of which later emerged as adults. The daily schedule which was worked out for the transfer of jars should help to explain how this material was handled.

Table II. DAILY SCHEDULE FOR TRANSFER OF BROOD JARS, CONTAINING BROOD OF THE WESTERN PINE BEETLE.

Time of change	Container number										
	1	2	3	4	5	6	7	8	9	10	11
	12	13	14	15	16	17	18	19	20	21	22
	23	24	25	26	27	28	29	30	31	32	33
	34	35	36	37	38	39	40	41	42	43	44
	45	46	47	48	49	50	51	52	53	54	55
	Temperature										
# 9 a.m.	40	40	40	40	40	40	75	75	75	75	75
11 a.m.	75										40
1 p.m.		75								40	
3 p.m.			75						40		
5 p.m.				75				40			
7 p.m.					75		40				
9 p.m.						75					

At 9 a.m. all specimens are returned to original temperatures

Explanation of chart:

Jars 1, 12, 23, 34, and 45 are placed at 40 degrees at 9 a.m. each morning and at 75 degrees at 11 a.m. Likewise the other columns of jar numbers follow the changes indicated below them at the periods indicated.

It will be noticed from table II that jars of mature larvae were so transferred as to give a complete series of exposures of two hours variation from two to twenty two hours daily at a high temperature favorable for development. Likewise this series reversed resulted in exposures at low temperatures below development of from two to twenty two hours daily. Many of these transfers to different compartments continued over a period of fifty days. Any apparent brood development was noted and recorded daily.

It was recognized that when jars of insects were transferred from a temperature of 40 to one of 75 degrees and visa versa there would be considerable lapse of time before they reached the surrounding air temperature. In order to measure this lag, thermometers were placed in four of the jars and readings taken every fifteen minutes until adjustment of temperatures had occurred. It was found that changes in both directions required but one hour for completion and therefore lag did not affect the experiments. Any loss in development due to lag following a transfer from 40 to 75 degrees would be made up in the one from 75 to 40 the degree compartment.

Since a temperature of approximately 50 degrees F. was determined to be the point at which development of the western pine beetle began, it has been possible to compute hour-degrees of effective temperatures. For example one degree of temperature above the zero of development, enduring for a period of an hour, constitutes an hour-degree.

Results of three series of alternating temperature experiments using 1680 mature larvae are tabulated and presented in table III. Also the rate of brood development of this insect is compared with the hour-degrees of cumulative temperatures in graph I.

TABLE III. Brood development of (*Dendroctonus brevicomis* Lec.
as affected by temperature
(prepupal larvae to adults)

Exposure per day at 25° F.	No. insects	Percent Mortality	First pupae		Average pupae		Pupae to adult average		First adults		Mature larvae to most pupae		Mature larvae to adult average		Larvae to final adults	
			Days Expos.	Hour deg.	Days Exp.	Hour deg.	Days Exp.	Hour-deg.	Days Exp.	H. deg.	Days Exp.	Hour degrees	Days exp.	Hour degrees	Days exposure	Hour degrees
22 Hrs.	150	32%	1.6	916	5.9	3240	7.5	4125	8.7	4812	8.6	4766	13.4	7370	19.0	10,450
20 hrs.	150	26%	2.0	1000	6.9	3450	8.0	4000	9.7	4850	11.0	5500	14.9	7450	20.7	10,375
18 hrs.	150	30%	1.8	966	7.3	3285	8.5	3825	10.3	4612	11.6	5223	15.3	7110	22.0	9,900
16 hrs.	150	23%	2.2	900	7.8	3120	10.5	4100	11.2	4500	12.0	4800	15.2	7220	21.5	9,675
14 hrs.	150	33%	3.3	1166	9.0	3150	10.9	3825	13.7	4812	14.3	5016	19.9	6,975	26.7	9,362
12 hrs.	150	32%	4.0	1200	10.3	3090	13.9	4170	16.0	4800	18.0	5400	24.2	7,260	34.0	10,200
10 hrs.	150	22%	3.9	966	12.2	3053	16.0	4000	18.2	4552	19.6	4916	28.0	7,050	42.0	10,500
8 hrs.	150	—	4.0	800	18.5	3660	23.5	4700	24.7	4950	25.5	5300	41.3	8,360	—	—
6 hrs.	150	—	6.3	950	22.0	3300	29.0	4350	32.0	4800	—	—	51.0	7650	—	—
4 hrs.	150	—	10.	1000	—	—	-	—	—	—	—	—	—	—	—	—
2 hrs.	150	—	21.	1050	—	—	-	—	—	—	—	—	—	—	—	—
average	Total 1650	31%		919		3260		4121		4744		5127		7,382		10,066

From the above table the days and hours exposure of different lots of larvae and subsequent development to more advanced stages can be very easily seen. Brood mortality in all of the containers was remarkably uniform, averaging slightly over 30 per cent. It will be noted that first pupae appeared from 2 to 21 days according to the hours exposure per day, and that some variation is also shown in the hour-degrees of development. This difference may be due to previously encountered temperatures of which we have no record. Other temperature summations are so uniform that they indicate an error in this first column.

Average pupae indicated by the time when the greatest number of larvae transformed to pupae averaged from about 6 to 22 days according to hours exposure per day, but when effective hour-degrees are summated they are strikingly close together (about 3200).

Average pupae to average adult, the time elapsing between transformation of largest number of larvae to pupae and transformation of largest number of pupae to adults also varies in days from 7 to 29 but as shown from computed hour-degrees development depends uniformly on exposure to temperature (4000 hour-degrees). The appearance of first adults also follows this same trend (4700 hour-degrees). Furthermore the summations of overlapping brood stages such as mature larvae to most pupae, mature larvae to average adults and larvae to final adults all result in approximately the same number of hour-degrees for a specific developmental stage. Because of the normal lag found in growth of some individuals final summations are often inclined to be somewhat out of line, but the average should present a more accurate picture of conditions.

A summation of the hour-degrees of effective temperature necessary for development from mature larvae to final adults at different constant temperatures as determined with 1125 specimens proved to be about 10,000 in all cases which had the time for completion. This agrees closely with similar summations obtained at alternating temperatures. Table III is the summation of alternating temperatures and table IV the summation of different constant temperatures. The hour-degrees obtained in both experiments for development of mature larvae to final adults is about 10,000.

Table IV

Effect of different constant temperatures on brood development of the western pine beetle

Temperature degrees F.	Number insects	Mortality per cent	Larvae to final adults Days exp.	Hour-degrees	Remarks
98° - 106°	125	100	10 days		
93 - 97°	125	100	19 "		
83 - 87°	125	52.2	12 "	10,080	
73 - 77°	125	44.1	17 "	10,200	
65 - 75°	125	30.0	21 "	10,080	
58 - 63°	125	54.0	42 "	10,080	
50 - 54°	125	46.0	41 "	—	15 pupae
38 - 42°	125	40.0	47 "	—	No development
34 - 38°	125	36.0	47 "	—	No development

At a constant temperature of 85 degrees the time required for all larvae to pass through the pupal stage and transform to adults was but twelve days. The number of days necessary for this degree of development increased until it required forty two days at 60 degrees. The time required for development of larvae to adults in hour-degrees was always about 10,000. This held true regardless of the manner of application of effective temperatures.

Alternating temperatures appeared to have no stimulating effect upon brood development. It depended directly upon the application of effective temperatures.

Comments

Intensive studies on the effect of temperature upon the rate of brood development of the western pine beetle have given us some pretty definite information upon this point. We have determined the point at which development begins as the temperature rises and at which it ceases as the temperature falls. We know that the rate of brood development depends directly upon the hour-degrees of effective temperature. We were also able to determine that alternating high and low temperatures do not tend to accelerate brood development. Furthermore, the range of optimum development as determined by the most insects produced has been pretty well established. Finally, the high lethal temperature preventing development of this insect has been determined.

Similar intensive studies on temperature and its effect upon some of our other more important forest insects would add much to our knowledge of their activities.

It is felt that the value of some of the findings on effect of temperature on brood development may have been minimised by the unsatisfactory phloem moisture conditions prevailing in the infested logs and blocks used. Successful control of phloem moisture in infested blocks under laboratory conditions would greatly add to the value of the work already done on brood development. Some satisfactory method of increasing evaporation from the blocks thru thorough ventilation could probably be evolved from a few empirical tests. More positive experiments on the effect of controlled phloem moisture and atmospheric humidity, especially the former, should precede or at least accompany nutritional studies on this insect. The two phases are apparently closely inter-related and might well be investigated together.

Conclusions

From the foregoing brood study on development of the western pine beetle a few tentative conclusions may be drawn.

Brood development of this insect begins at about fifty degrees Fahrenheit.

The rate of brood development increases directly with the temperature up to about eighty five degrees Fahrenheit.

Constant temperatures of ninety five and above, if sufficiently maintained, are fatal to all stages.

Most rapid development occurs at about eighty five degrees, but most successful development from the standpoint of greatest numbers of insects produced is in the vicinity of seventy to seventy five degrees.

Phloem moisture of infested felled material increases or remains abnormally high in all cases except at high lethal temperatures where some drying occurs.

The western pine beetle develops very poor broods under the range of temperature and moisture conditions obtained in blocks in the laboratory and slash in the field.

Failure of broods to develop at low temperatures below fifty degrees Fahrenheit and at high temperatures above ninety five degrees are probably due to the effect of limiting temperatures.

Brood failures occurring within favorable temperature zones are probably due to excessive moisture of the inner bark or some factor closely associated with it. Malnutrition and an abundant green <u>Penicillium</u> are probably two very important factors.

Daily changes in temperature appear to have no stimulating effect on the rate of brood development.

A definite number of hour-degrees of effective temperatures are necessary for the development of a specific brood stage of the western pine beetle.

A thermograph record of early spring and summer temperatures would probably be very useful in determining the time of emergence of overwintering broods in any particular area.

Fig. 1

Fig. 2

Fig. (1) Pine blocks used in brood study of western pine beetle.
Fig. (2) Pine blocks and infested bark in cage used for obtaining attack.

Fig. 3

Fig. 4.

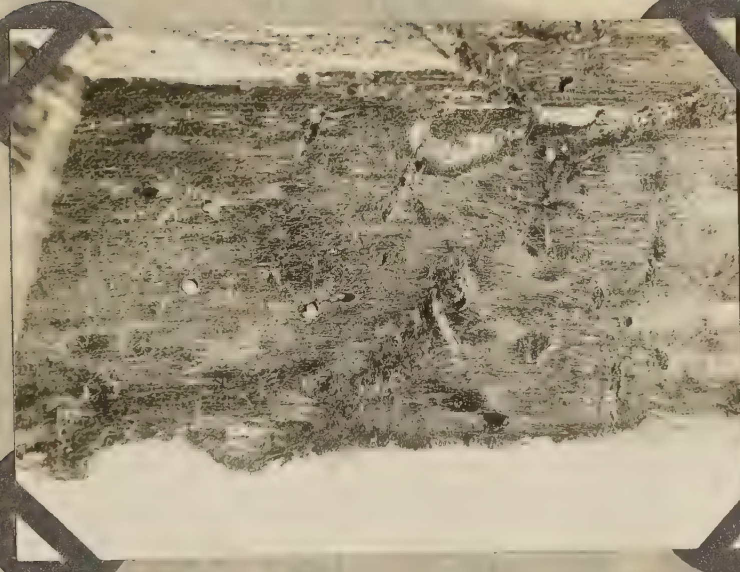


Fig. (3)-Infested bark, jars and petri dishes containing insects used in brood development study.

Fig. (4)-Inner bark from infested block showing tiny larvae seven weeks old (Note. most brood here dead).

Fig. 5.

Fig. 6.

Fig. (5) D.b. eggs and newly hatched larvae much enlarged on blotting paper in controlled temperature chamber.
Fig. (6) D.b. tiny larvae, x2 dead larvae and abnormally long larval galleries of infested block at 95° F.

Fig. 7.

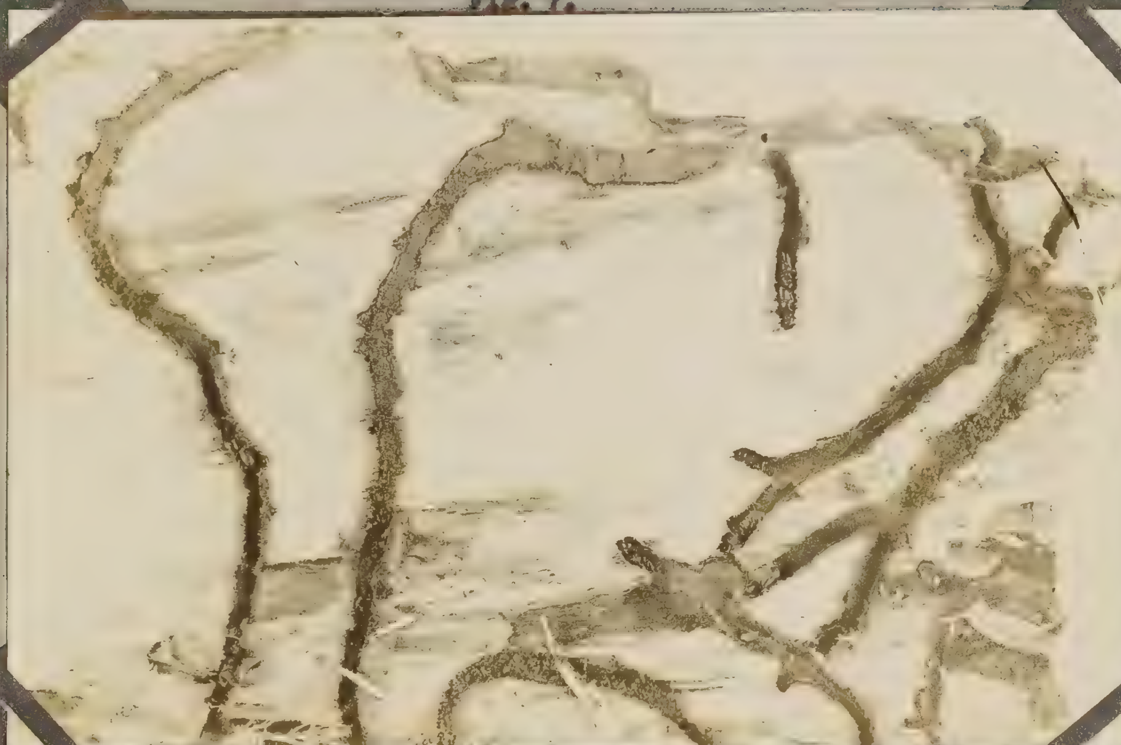
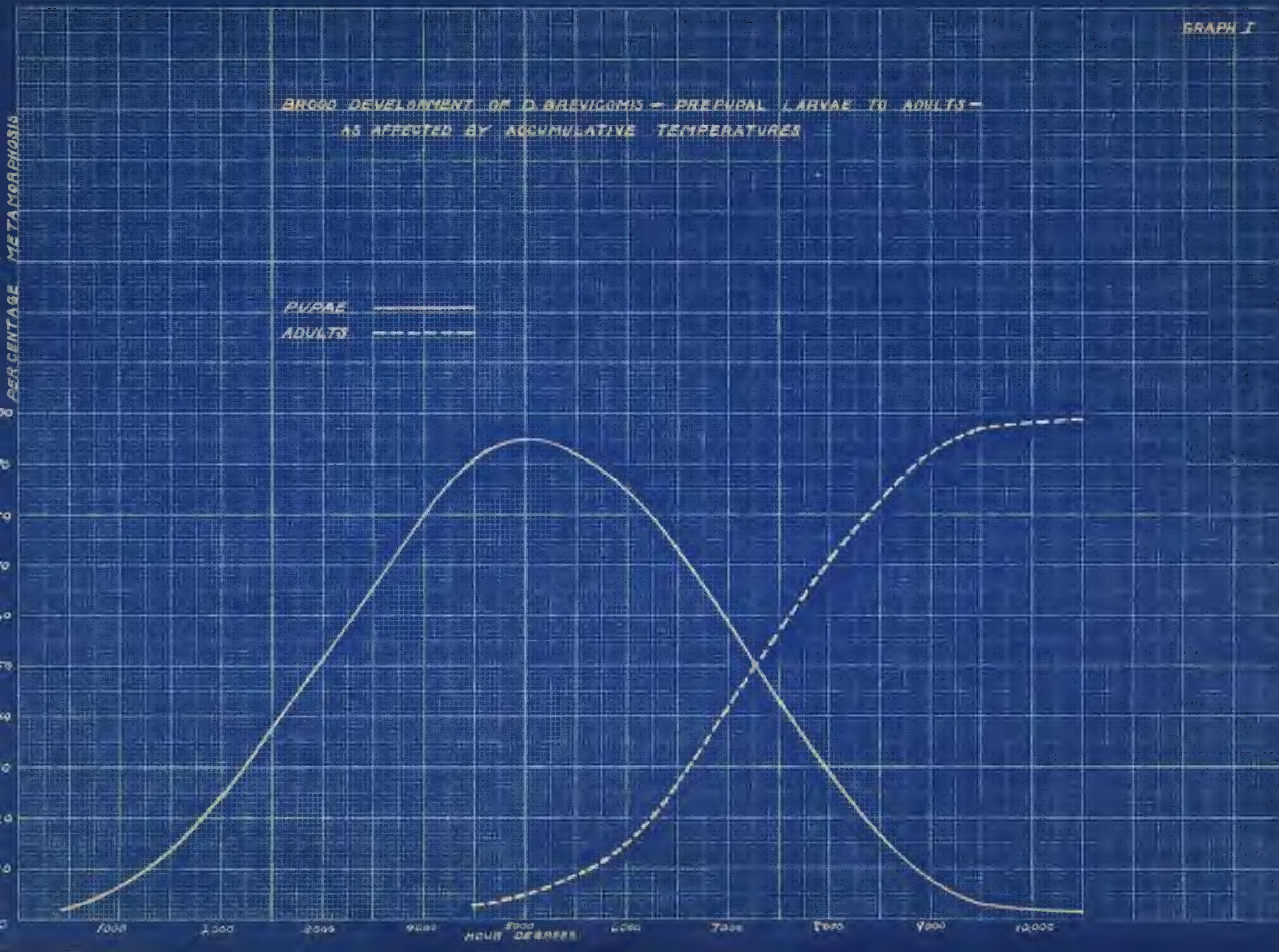
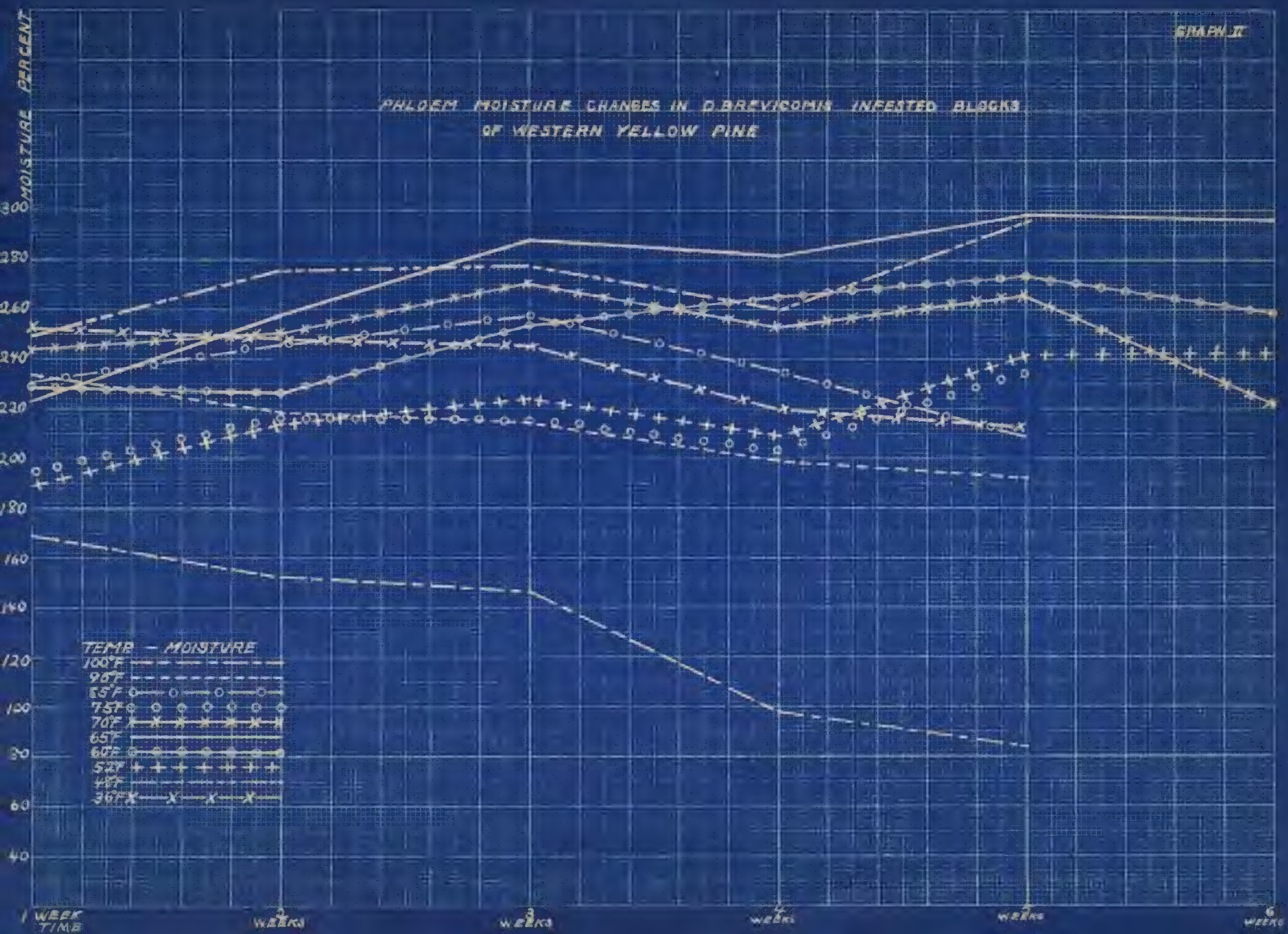
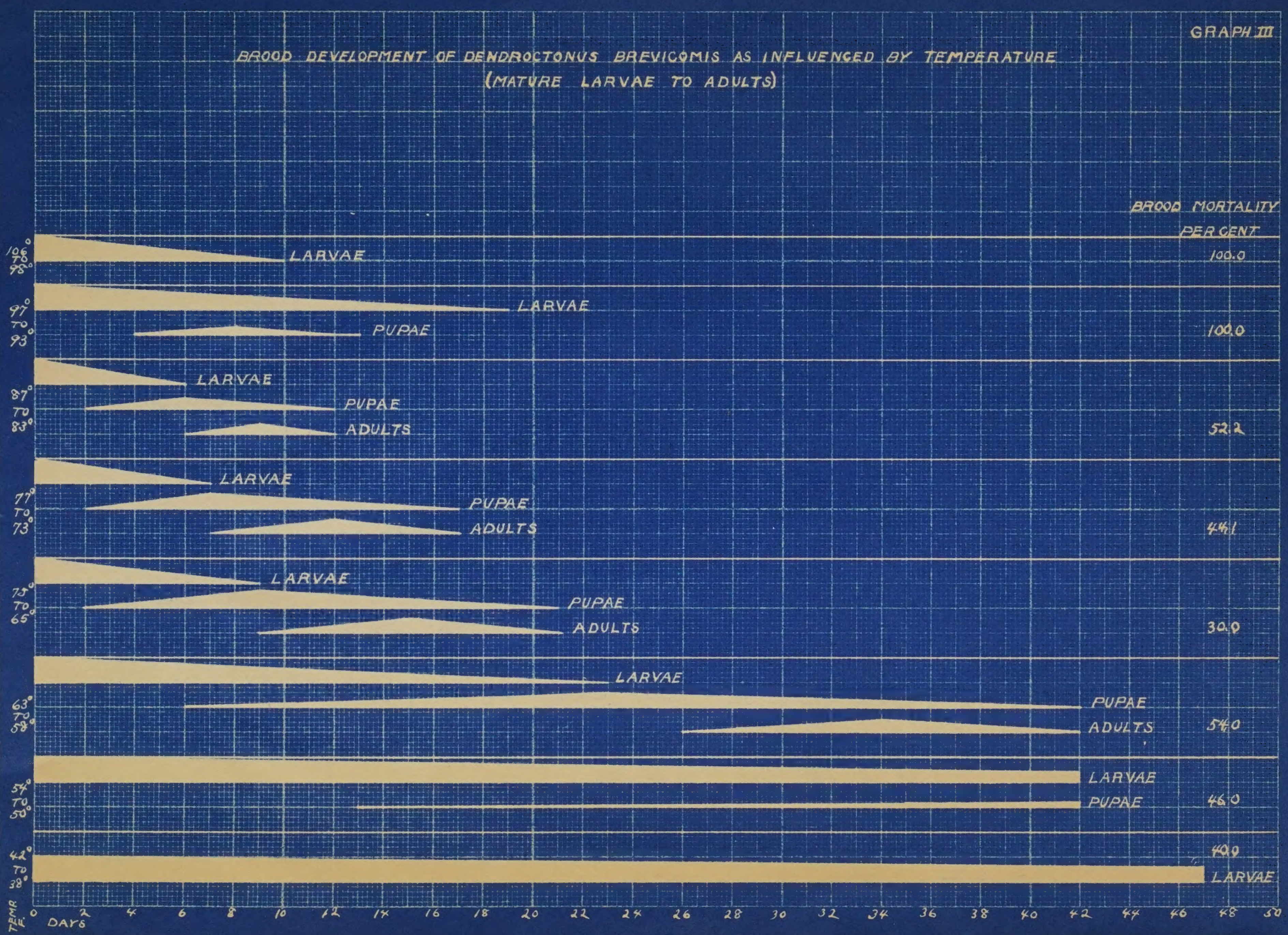


Fig. (7) Showing D.b. galleries and egg niches and dead adults in infested block from constant temperature chamber of 100° F.


GRAPH I
BROOD DEVELOPMENT OF D. BREVICOMIS – PREPUPAL LARVAE TO ADULTS –
AS AFFECTED BY ACCUMULATIVE TEMPERATURES
PUPAE
ADULTS
PER CENTAGE METAMORPHOSIS
HOUR DEGREES
1000
2000
3000
4000
5000
6000
7000
8000
9000
10,000


GRAPH II
PHLOEM MOISTURE CHANGES IN D. BREVICOMIS INFESTED BLOCKS
OF WESTERN YELLOW PINE
MOISTURE PERCENT
300
280
260
240
220
200
180
160
140
120
100
80
60
40
1 WEEK
TIME
2 WEEKS
3 WEEKS
4 WEEKS
5 WEEKS
6 WEEKS
TEMP - MOISTURE
100°F
75°F
70°F
65°F
60°F


GRAPH III
BROOD DEVELOPMENT OF DENDROCTONUS BREVICOMIS AS INFLUENCED BY TEMPERATURE
(MATURE LARVAE TO ADULTS)
BROOD MORTALITY PER CENT
106° TO 98°
LARVAE
100.0
97° TO 93°
LARVAE
PUPAE
100.0
87° TO 83°
LARVAE
PUPAE
ADULTS
52.2
77° TO 73°
LARVAE
PUPAE
ADULTS
44.1
75° TO 65°
LARVAE
PUPAE
ADULTS
30.0
63° TO 58°
LARVAE
PUPAE
ADULTS
54.0
54° TO 50°
LARVAE
PUPAE
46.0
42° TO 38°
LARVAE
40.0
TEMP. F.
DAYS
0 2 4 6 8 10 12 14 16 18 20 22 24 26 28 30 32 34 36 38 40 42 44 46 48 50